

Patelloida chamorrorum spec. nov.: A New
Member of the Tethyan *Patelloida profunda*
Group (Gastropoda: Acmaeidae)

by

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Abstract. *Patelloida chamorrorum* spec. nov. from the Mariana Islands in the tropical western Pacific is described. The new species is a member of an ancient patellacean group that first appeared in the Eocene of the Paris Basin, and is today represented by scattered endemic populations throughout the tropics. This group, typified by *Patelloida profunda* Deshayes, is diagnosed for the first time and its distribution in space and time documented; members of the group are closely associated with calcareous substrates. *Patelloida deshayesia* nom. nov. is proposed as a replacement name for the homonym *Patella glabra* Deshayes.

INTRODUCTION

ONE OF THE MOST common gastropods of the rocky intertidal zone in Guam and other islands in the southern Marianas is an undescribed patellacean limpet of the genus *Patelloida*. Its recognition is significant not only because it contributes to a better understanding of the fauna of the Mariana Islands, but also because the new species is a member of an ancient lineage whose living members are scattered as endemic populations throughout the tropics. In this paper we describe the new species and outline its relationship to other living and fossil members of the *Patelloida profunda* group, a Tethyan clade that appears to be specialized for life on calcareous substrata.

Abbreviations are as follows: AHF—Allan Hancock Foundation (on permanent loan to LACM); ANSP—Malacology Department, Academy of Natural Sciences, Philadelphia, PA; CASIZ—Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, CA; LACM—Malacology Section, Natural History Museum of Los Angeles County, Los Angeles, CA; UCMP—Museum of Paleontology, University of California,

Berkeley, CA; USNM—Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C.

SYSTEMATICS

ACMAEIDAE Forbes, 1850

PATELLOIDINAE Oliver, 1926

Shell: Shell composed of four layers. Outer surface of shell and interior margin complex prismatic. Next inner layer concentric crossed-lamellar, followed by myostracum, and radial crossed-lamellar layers.

Radula: Lateral teeth three pairs, uni- or multicuspid; marginal teeth two pairs or lacking. Ventral plates complex or simple.

Animal: Eyes present. Gut looping complex or highly simplified. Pericardial sac penetrated by rectum in some species. Excretory organs paired or with single right excretory organ and brood chamber. Gill typically present in nuchal cavity, but may be replaced by secondary gill in mantle groove, or absent.

Patelloida Quoy & Gaimard, 1834

Patelloida QUOY & GAIMARD, 1834:349, type-species by subsequent designation of GRAY, 1847:158, *Patelloida rugosa* Quoy & Gaimard, 1834.

Shell: Typically stout, with thick intermediate area composed of concentric crossed-lamellar layer. Sculpture variable but radial component usually present and concentric growth line sculpture typically threadlike and pronounced in complex prismatic layer.

Radula: Lateral teeth variable in size and shape; marginal teeth two pairs, cusps complex. Ventral plates complex; sutures, anterior processes and/or lateral extensions present in most taxa.

Animal: Gut looping complex; two excretory organs, one on either side of rectum; gill present in nuchal cavity. Oral lappets present in some species. Mantle edge often thickened with large tentacle/gland complexes.

Cretaceous to Recent. Past and present tropical and warm-temperate seas.

The *Patelloida profunda* Group

CHRISTIAENS (1975:93) first recognized the "*Patelloida profunda* Group," and referred several species to it, based on their resemblance (Table 1). The group is characterized for the first time as follows:

Light-colored shells of moderate to high profile. All slopes typically straight with rounded radial ribs; brown radial markings common. Ventral plates of radula complex with strong lateral processes and sutures; lateral teeth typically of equal size and shape. Recent species closely associated with calcareous substrates in tropical nearshore environments.

Patelloida chamorrorum

Lindberg & Vermeij, spec. nov.

(Figures 1–4, 10–12)

Patelloida flammea Quoy & Gaimard: HEDLEY, 1915:713 [non Quoy & Gaimard, 1834].

Patelloida sp.: VERMEIJ, 1971:316; VERMEIJ *et al.*, 1984 [in press].

Acmaea conoidalis auctt. [non Pease, 1868].

Shell (Figure 1): Shell of medium profile, apex slightly anterior of center. All slopes straight to weakly convex. Sculpture of approximately 35 primary ribs, smaller secondary ribs intercalated between most primary ribs. Radial sculpture overlain by rugose, concentric growth lines creating pustules on some primary ribs. Exterior of shell dirty white with 13 dark radial rays. Rays red-brown and intermittent on eroded portions of the shell. Interior margin white with dark markings corresponding to exterior rays. Intermediate area translucent white, with vague exterior rays. Central area strongly outlined by opaque white callus, tinted with orange-yellow.

Radula (Figures 2, 3): First pair of lateral teeth set

Table 1

Recent members of the *Patelloida profunda* group.

Taxon	Distribution
<i>Patelloida profunda</i>	Western Indian Ocean
<i>Patelloida profunda albonotata</i>	South Africa
<i>Patelloida profunda ivani</i>	Northwestern Australia
<i>Patelloida profunda mauritiana</i>	Mauritius
<i>Patelloida profunda omanensis</i>	Gulf of Oman
<i>Patelloida calamus</i>	Temperate Southern Australia
<i>Patelloida chamorrorum</i> *	Southern Marianas
<i>Patelloida conoidalis</i>	French Polynesia
<i>Patelloida pustulata</i> *	Caribbean
<i>Patelloida semirubida</i> *	Panamic
<i>Patelloida</i> sp.*	Java and New Guinea
<i>Patelloida</i> sp.*	Palau Group

* Newly assigned species.

close together on anterior edge of basal plates; cusps blunt. Second pair of lateral teeth directly posterior to first pair; cusps rounded. Third pair of lateral teeth lateral to second pair; cusps rounded. Lateral tooth edge elongated forming lateral extension that terminates near edge of ventral plates. Marginal teeth two pairs, cusps spoonlike; shafts elongate, terminating near middle of next posterior tooth row. First lateral plates tear-drop shaped, affixed to rounded anterior extension of the basal plate. Second lateral plates posterior to first plates; posterior edges straight, separated from third lateral plates by partial suture. Third lateral plates rounded. Ventral plates highly complex with anterior processes, lateral extensions, and strong anterior, posterior and lateral sutures. Posterior medial portion of plates marked with semicircular suture. Anterior edges of ventral plates concave, posterior edge convex.

Animal: Pigmentation lacking. Oral lappets present on snout, well-developed laterally and posteriorly; however, anterior portion of lappets weak (Figure 4). Mantle edge thickened with numerous large tentacle-gland complexes. These structures correspond to the fine crenulations around the perimeter of the aperture. Looping of the gut complex, intestine passing over digestive gland several times; eight sections of the intestine and stomach visible in some specimens (=4 loops).

Holotype dimensions: Length 14.1 mm, width 11.2 mm, height 5.9 mm.

Type locality: *Mariana Islands:* Guam; Asanite Bay (13°20'N, 144°46'E), leg. G. J. Vermeij, 10 July 1970.

Type material: Holotype UCMP 37522; 6 paratypes UCMP 37523. Paratypes have also been deposited in the collections of the USNM and LACM.

Distribution: *Western Pacific:* Mariana Islands; Cocos Island (AHF Acc. 1022)(13°14'N, 144°39'E), Guam [Type locality], Saipan (LACM 101634) (15°11'N, 145°45'E), and Tinian Island (LACM 101633)(14°58'N, 145°38'E).

Material examined: 18 lots, more than 100 specimens.

Etymology: The specific name, *chamorrorum*, is in honor of the Chamorro, the people of the Marianas.

Discussion: Other patellacean limpets in the Marianas that could be confused with *Patelloida chamorrorum* include small encrusted specimens of *Patella flexuosa* Quoy & Gaimard, 1834, and *Cellana radiata orientalis* (Pilsbry, 1891). *Patella flexuosa* has a lower profile and more irregular margin than *P. chamorrorum*. The central area of *P. flexuosa* is colored with orange-yellow; in *P. chamorrorum* the central area is only tinted. Radulae of the two species are quite different. *Patella flexuosa* has three pairs of marginal teeth, six pairs of lateral teeth, and a central tooth (3-6-1-6-3); *P. chamorrorum* has two pairs of marginal teeth, three pairs of lateral teeth, and lacks a central tooth (2-3-0-3-2). *Patella flexuosa* has a secondary gill; *P. chamorrorum* lacks a secondary gill.

Cellana radiata orientalis, which co-occurs with *Patella flexuosa* on wave-dashed algal ridges, differs from *Patelloida chamorrorum* in several important ways. The *Cellana* species has an irregular shell surface overlain by numerous, coarse riblets, and because of the uneven shell surface, the shell margin is also irregular. In *C. radiata orientalis* the shell structure is nacre-like (foliated) rather than porcelainous as in *P. chamorrorum*. The radular tooth formula of *C. radiata orientalis* is 3-2-0-2-3 and lacks a nuchal cavity gill but does have a secondary gill.

In their original description of *Patelloida flammea*, QUOY & GAIMARD (1834:354) reported this species from both Hobart-Town, Tasmania, and from Guam. HEDLEY (1915) proposed that *P. flammea* should be restricted to a species from Guam, and that the Tasmanian species was actually *Patella mixta* Reeve, 1855. However, IREDALE (1924) and OLIVER (1926) have pointed out that Quoy & Gaimard selected the Tasmanian species as the typical form of *P. flammea* (see PONDER & CREESE [1980] for a recent discussion of the identity of *P. flammea*). We agree that the species described and illustrated by Quoy & Gaimard as *P. flammea* is not from Guam, and more specifically, is not the species described herein as *P. chamorrorum*. QUOY & GAIMARD (1834) illustrated the snout of *P. flammea* (pl. 71, fig. 24). This drawing clearly shows weakly developed oral lappets (Figure 5); the oral lappets of *P. chamorrorum* are strongly developed (Figure 4), and the difference between these two states is too extreme to be a preservational artifact.

Specimens of the new species *Patelloida chamorrorum* have been confused with members of the *Patelloida profunda* (Deshayes, 1863) group. CHRISTIAENS (1975:93) referred *P. profunda* and the subspecies *P. p. albonotata* (Smith, 1901), *P. p. mauritiana* (Pilsbry, 1891), *P. p. omanensis* Christiaens, 1975, *P. p. ivani* Christiaens, 1975, plus *P. conoidalis* (Pease, 1868) and *P. calamus* (Crosse & Fischer, 1864), to this group stating that they had "a certain resemblance and probably the same ancestor." We

concur with Christiaens and refer *P. chamorrorum* to this group. *Patelloida chamorrorum* is distinguished from other members of the group by shell characters, external anatomy, and radular characters.

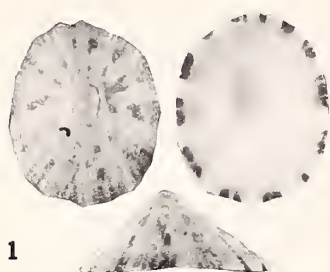
Patelloida chamorrorum has been often labeled in museum collections as *P. conoidalis* (Figure 6). Rib number and strength clearly define these two species. In *P. conoidalis* there are more ribs (50-60+) and the primary ribs are therefore narrower. The shell of *P. conoidalis* also has a stronger concentric sculpture that sometimes produces a cancellate pattern and the shell lacks coloration (no dark rays or red markings). Both species can have orange-yellow intermediate areas and the thickened central area can also be tinted. In the field the two species can be quickly distinguished by the shape of the oral lappets on the snout (cf. Figures 4, 7).

Patelloida chamorrorum differs from the nominal species of the group, *P. profunda*, by having fewer riblets, a more central apex, and by lacking the brown central area and white and light brown rays on the exterior shell surface. *Patelloida chamorrorum* differs from *P. calamus* (Figure 8) and *P. p. mauritiana* (Figure 9) in similar ways. Both *P. calamus* and *P. p. mauritiana* have more ribs (70-80+) than *P. chamorrorum* (30-40). In *P. calamus* the primary and secondary ribs are not well differentiated; both *P. chamorrorum* and *P. p. mauritiana* have distinct primary and secondary ribs. *Patelloida p. mauritiana* differs from *P. chamorrorum* by (1) having heavier, thread-like concentric growth lines that produce pustules at some intersections with the radial ribs, and (2) being dingy white in color and lacking radial rays and red markings. *Patelloida calamus* has fewer (6-8) dark rays than *P. chamorrorum*. In *P. calamus* the central area is sometimes red-pink; in *P. p. mauritiana* the intermediate area is often yellow-orange and thickened as in some specimens of *P. chamorrorum* (see Remarks below).

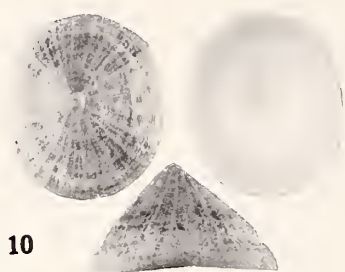
The radula of *Patelloida chamorrorum* clearly distinguishes it from other members of the *P. profunda* group. No previously recognized member of the *P. profunda* group has lateral extensions on the third lateral teeth (Figure 2).

Although the radulae are distinct in all members of this group, we are impressed by the similarities in both ventral plate and radular tooth morphologies. The differences between species in this group are more subtle than occur in other Patelloidinae (cf. PONDER & CREESE, 1980; LINDBERG, 1983) and in other genera (e.g., *Collisella*, *Lotia*, *Notoacmea*) (cf. MOSKALEV, 1970; PONDER & CREESE, 1980; LINDBERG & McLEAN, 1981; LINDBERG, 1981).

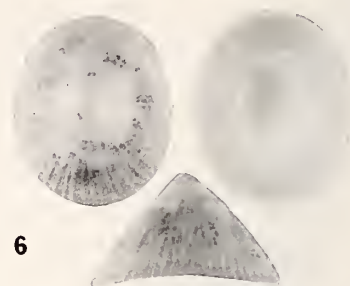
Remarks: There is inter-island variation in shell characters. Specimens from Tinian are slightly larger (up to 25+ mm long) and have higher profiles than those from Guam and the more southern islands (Figure 10). These specimens have shells similar to those of *Patelloida conoidalis* and *P. p. mauritiana*. Specimens from the more southern Marianas tend to be lighter in color and have more



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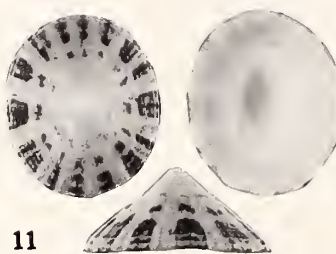
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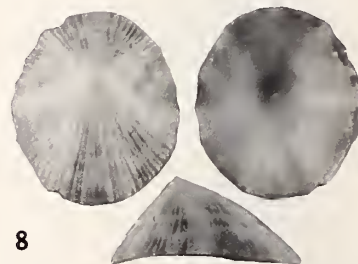
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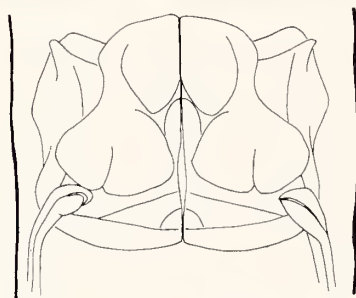
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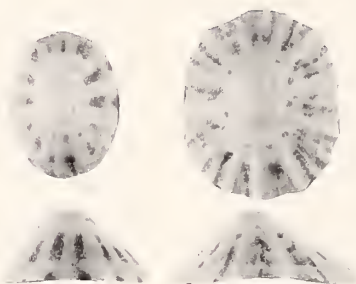
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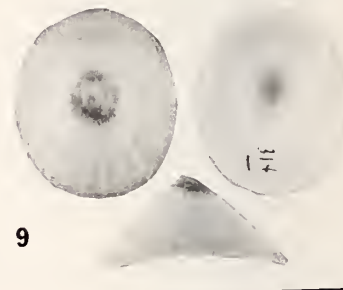
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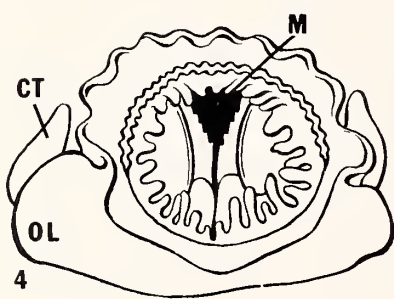
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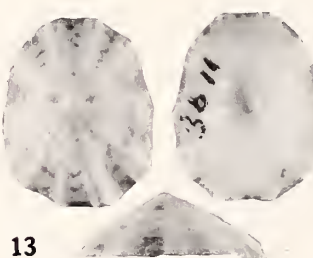
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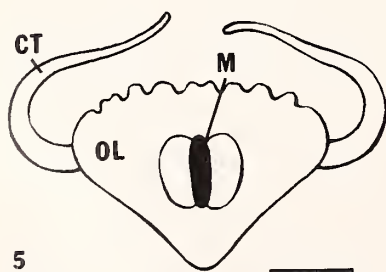
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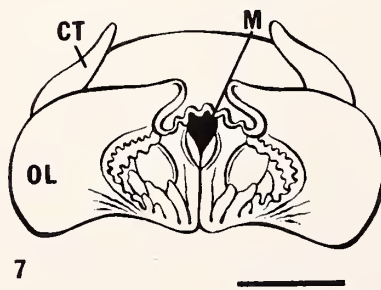
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16

vivid markings (Figure 11). While these markings are similar to those of *P. calamus* and other members of the *P. profunda* group (CHRISTIAENS, 1975), they most resemble the Recent New World *Patelloida*, *P. pustulata* (Helling, 1777) and *P. semirubida* (Dall, 1914).

Juvenile shells of *Patelloida chamorroorum* have fewer ribs than the larger shells, and the radial color pattern is typically present (Figure 12). The intermittent red markings, which are found on some of the larger shells from Guam, are readily apparent on juvenile shells. These markings appear to be identical to the red markings found on some specimens of *P. pustulata* from the Caribbean (Figure 13).

Ecology and biogeography: *Patelloida chamorroorum* is an abundant limpet on the middle and upper shore of all the southern Mariana Islands, where it occupies pits (presumably of its own making) in the limestone. The chiton *Acanthopleura gemmata* (Sowerby, 1825) typically occurs with *P. chamorroorum*. We believe that *P. chamorroorum* is restricted to limestone shores. The species is not found on the volcanic shores of southwest Guam (VERMEIJ, 1971), and it is absent from the nine volcanic northern Mariana Islands (VERMEIJ *et al.*, 1984) (both as *Patelloida* sp.).

Patelloida chamorroorum is one of only a small handful of marine mollusks that are endemic to the southern Marianas. The only other confirmed example is the littorinid *Echininus viviparus* Rosewater, 1982, which, like *P. chamorroorum*, is an upper-shore species. *Echininus viviparus* is chiefly, but not exclusively, on limestone (VERMEIJ, 1971; ROSEWATER, 1982). Another possible endemic species is the small neritid *Nerita guamensis* Quoy & Gaimard, 1834. This species, or forms very much like it, is distributed in a disjunct fashion in the Philippines, Fiji, Samoa, the Ryukyus, the Izu Islands, and the northern and southern Marianas, and perhaps also the Natal coast of southeastern Africa. *Nerita guamensis* varies greatly from place to

place in the southern Marianas, especially in color, and lives with *E. viviparus* on the upper shore. It is striking that none of the upper-shore endemics of the southern Marianas are found in, or are closely related, to species inhabiting the atolls of the Marshall Islands, whose fauna is in most other respects similar to the Marianas. The disjunct distribution of the stocks to which the endemics belong suggests that the Mariana Islands may serve as a refuge for previously more widespread taxa in the tropical western Pacific.

DISCUSSION

The recognition of *Patelloida chamorroorum* in the Marianas and of its membership to the *Patelloida profunda* group caused us to examine closely the anatomical and shell characters of similar Recent members of the genus *Patelloida* and the shell characters of fossil species. From this work we have recognized additional Recent members of the *P. profunda* group in Indonesia, the tropical eastern Pacific, and Caribbean. Fossil members were identified from the Paleogene of Europe and the Neogene of the Caribbean.

In addition to the species listed by CHRISTIAENS (1975) and *Patelloida chamorroorum*, we would include *Patelloida* sp. (Java and New Guinea) (Figure 14), *Patelloida* sp. (Palau Group), *Patelloida semirubida* (Panamic), and *Patelloida pustulata* (Caribbean) in the *P. profunda* group (Table 1). Fossil members of this group are present in the Eocene rocks of the Paris Basin (*Patelloida centralis* [Deshayes, 1861] [Figure 15], *Patelloida deshayesia* nom. nov. [Figure 16]) and in materials recently collected in the Dominican Republic by Dr. Peter Jung and colleagues (*Patelloida* sp.) (Lindberg, unpublished data). Thus, Recent members of the *Patelloida profunda* group are distributed eastward from the east coast of Africa to the Caribbean. In the Eocene the group probably extended farther east to the Paris Basin of France, a clear and definite

Explanation of Figures 1 to 16

Scale bar = 10.0 mm except as noted.

Figures 1 to 4. *Patelloida chamorroorum* spec. nov. Figure 1. Holotype, UCMP 37522; Asanite Bay, Guam. Figures 2 and 3. Radular tooth and lateral plate morphology, LACM 77-16; Pago Bay, Guam. Scale bar = 0.1 mm. Figure 4. Ventral view of snout; oral lappets (ol), cephalic tentacles (ct), mouth (m) (museum data same as Figures 2 and 3). Scale bar = 1.0 mm.

Figure 5. Ventral view of snout of *Patelloida flammea*. Redrawn from QUOY & GAIMARD (1834; pl. 71, fig. 24). See Figure 4 for legend. Scale bar = 1.0 mm.

Figures 6 and 7. *Patelloida conoidalis*, LACM 69206; Henderson Island, Pitcairn Islands. Figure 6. Shell. Figure 7. Ventral view of snout. See Figure 4 for legend. Scale bar = 1.0 mm.

Figure 8. *Patelloida calamus*. Hypotype, UCMP 37524; Tumbay Bay, Australia. Scale bar = 5.0 mm.

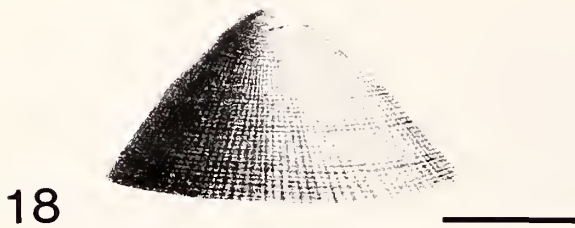
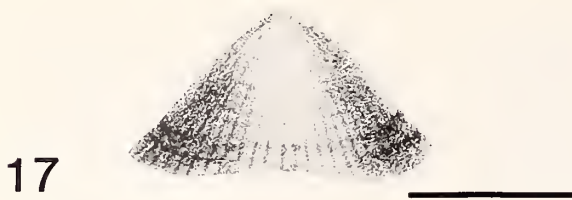
Figure 9. *Patelloida profunda mauritiana*. Hypotype, UCMP 37525; Mauritius.

Figures 10 to 12. *Patelloida chamorroorum* spec. nov. Figure 10. LACM 101628; Tinian Island. Figure 11. LACM 20342; Guam. Figure 12. LACM 77-3; Pago Bay, Guam. Scale bar = 5.0 mm.

Figure 13. *Patelloida pustulata*. LACM 35543; Bahama Islands.

Figure 14. *Patelloida* sp. Hypotype, UCMP 37526; Malinyping, Java.

Figures 15 and 16. Eocene *Patelloida* from the Paris Basin, France. Figure 15. *Patelloida centralis*. Hypotype, UCMP 37527. Scale bar = 5.0 mm. Figure 16. *Patelloida deshayesia* nom. nov. Hypotype, UCMP 37528. Scale bar = 5 mm.



Explanations for Figures 17 and 18

Scale bar = 10.0 mm.

Figure 17. Original illustration of *Patelloida conoidalis* from PEASE, 1868; pl. 11, fig. 22. Recent, Rarotonga Island, Cook Islands.

Figure 18. Original illustration of *Patelloida centralis* from DESHAYES, 1861; pl. 5, fig. 3. Eocene, Paris Basin, France.

Tethyan distribution in space and time (VERMEIJ, 1978: 227).

We characterize members of the *Patelloida profunda* group as having light-colored shells of moderate to high profile; rounded radial ribs and brown radial markings are typically present. The Recent species have complex radular ventral plates with strong lateral processes and sutures, and the lateral teeth are typically of equal size and shape. The Recent species are closely associated with calcareous substrates; members of this group are typically found on the abundant calcareous substrates and debris that predominate in tropical nearshore environments.

The fossil species were first identified using shell structure; all are members of the Patelloidinae and their shell morphology is identical to Recent members of the *Patelloida profunda* group. On some Eocene specimens from the Paris Basin, radial color patterns, similar to those of the Recent species, are still present. However, one of the most striking examples is seen by comparing the original illustration of the Recent *P. conoidalis* with the original illustration of the Eocene *P. centralis* (cf. Figures 17, 18). The differences that appear in these two illustrations are less than the intraspecific differences in most Recent species.

The similar shell morphology of members of the *Patelloida profunda* group has been responsible for many of the misidentifications of the species discussed herein, including *P. chamorroorum*. As stated above, *P. chamorroorum* has been most often misidentified as *P. conoidalis*. This is also true for other members of this group in the Indo-

Pacific. The *Patelloida* sp. from Java and New Guinea has been previously identified as *P. conoidalis* (CERNOHORSKY, 1972:38; pl. 6; fig. 5) and CHRISTIAENS (1980:77) has referred it to "*P. conoidalis* aff." from Hong Kong. At this time we have not seen an indisputable specimen of *P. conoidalis* from any locality farther west than the Cook Island group (160°W), and we suspect that, as in the case of *P. chamorroorum* in the Marianas, each *P. profunda* member in a major island group will prove to be distinct at the specific level. Currently, there is insufficient material, particularly whole animals, to describe the species from Java and New Guinea. However, shell characters do appear to distinguish this species from both *P. conoidalis* and *P. chamorroorum*. Another member of the *P. profunda* group for which there is insufficient material occurs on limestone cliffs at Urukthapel in the Palau Group (Vermeij, personal observation). The Palau Group species has more numerous radial ribs than *P. chamorroorum*.

The presence of a member of the *Patelloida profunda* group in the East Indies results in an almost continuous distribution for this group across the Pacific Ocean and into the Indian Ocean. However, we are suspicious of the apparent absence of a member of this group in the more northern islands of the East Indies (Celebes, Borneo, Philippines). A possible member in the Philippines may be "*Acmaea lentiginosa*" Reeve, 1855, reported by HIDALGO (1904) from Marinduque and Mindanao and by FAUSTINO (1928) from Marinduque and Surigao. We have not seen any specimens from the Philippines that are similar to Reeve's species and his description lacks locality data.

ACKNOWLEDGMENTS

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APPENDIX

Patelloida deshayesia nom. nov.

Figure 16

While preparing this paper, we found that primary homonymy exists between *Patella glabra* Turton, 1806, and *Patella glabra* Deshayes, 1824. *Patella glabra* TURTON, 1806:572 [vol. 4] is an unrecognizable, unlocalized brown limpet with white ribs. *Patella glabra* [DESHAYES, 1824: 10] is an Eocene *Patelloida* from Paris Basin localities in

France, and a junior primary homonym of *P. glabra* Turton, 1806. Therefore, we propose the name *Patelloida deshayesia* nom. nov. to replace *Patella glabra* Deshayes. The specific name is in honor of G. P. Deshayes who eloquently monographed the limpets (and other mollusks) of the Paris Basin.

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